

external and internal causal factors determine the overall level of motivation by a multiplicative interaction (McFarland & Sibly 1975; Sibly 1975), feeding will continue indefinitely because external causal factors for drinking (i.e. water or knowledge of the existence of water) will be weak or absent, whereas both external and internal causal factors for feeding will be present.

With a time-sharing mechanism, thirst-motivated appetitive behaviour will be disinhibited after a short preliminary bout of feeding; but if the bird does not find water in the few seconds allotted to drinking, the feeding system will reassert its dominance. Thus, if food and water are simultaneously available, time-sharing allows the bird to achieve the finely balanced intake of food and water that is presumably optimal. But if food and water are not simultaneously available at relatively little cost, time-sharing prevents the bird from having to interrupt feeding at an early stage in order to engage in a prolonged search for water; or from becoming trapped in an indefinitely prolonged bout of feeding, which would lead to a serious water debt. Thus, time-sharing may in natural conditions combine the merits of disinhibition and inhibition, and allow more flexibility in the sequencing of behaviour than would either of these mechanisms acting alone.

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#### Shell Exchanges in Hermit Crabs: Aggression, Negotiation, or Both?

Intraspecific aggression is often viewed as one mechanism whereby competitive interactions between individuals are effected (Wilson 1975; Smith 1977). Since competition is operationally defined as the negative effects of the presence or activities of some individuals on the fitness of other individuals (Birch 1957), it seems implicit in the use of the term aggression that the result of the interaction will be that one animal gains at the expense of another.

Gastropod shells are a limiting resource for most hermit crab populations (Vance 1972; Bach et al. 1976) and the

ritualized shell fighting behaviour seen in most species (Hazlett 1966) reflects past selective pressure for the acquisition of these resource items. An earlier analysis of the situations stimulating initiation of a shell exchange (Hazlett 1970) focused only on the behaviour of the initiator. Initiating crabs always 'fought for' shells that were better fitting than the one they currently occupied, either in terms of shell weight or internal volume of the shell (Hazlett 1970).

However, it is possible that the non-initiating crab ('defender') may gain in an exchange. That is, the shell of the initiating crab may represent a better fit for the non-initiator than its presently occupied shell. If both participants gain from the exchange, the term negotiation may better describe the behavioural interactions than the term aggression.

Direct evidence for a mutual exchange has not been recognized in hermit crabs. However, evidence supporting such an idea would be that the length of shell-related interactions would be inversely correlated with the degree to which the non-initiator may gain from the exchange. To test this hypothesis, I have re-analysed data (Hazlett 1970) on shell exchanges in the hermit crab *Pagurus bernhardus*.

These data provide two kinds of information: (1) the regression lines between crab size and shell volume and weight when crabs are given free access to a large number of empty shells (from this one can calculate the preferred shell parameters for a given size crab) and (2) the crab size and shell parameters of pairs of individual crabs engaging in a shell exchange or attempted shell exchange. The deviation of each crab's present shell from the preferred shell parameters can be used as a measure of how motivated each crab may be to obtain a new shell. In addition, the deviation from the preferred shell size that would result for each crab if an exchange occurred can represent the motivation of each crab to engage in a particular shell exchange.

These deviations were calculated for each crab participating in a shell-related interaction. The number of raps (Hazlett 1966) executed by the initiator (mean = 48, range 0–390) was used as a measure of fight length. Data were obtained from 15 interactions in which a mutual exchange of shells took place and 26 interactions in which an exchange of shells did not take place (interaction terminated by initiator leaving). Multiple linear regression analyses were used to examine the variance in fight length.

As reported earlier (Hazlett 1970), there was no correlation between the difference in sizes of the participants and the number of raps executed. In the present analyses, significant relationships were found between interaction length and only two of the motivational variables (Table 1): (1) the deviation of the non-initiator's shell from its preferred shell weight and (2) the deviation of the initiator's shell from the preferred shell volume of the non-initiator. Thus the greater the deviation in weight of the non-initiator's shell and the better (in volume) the initiator's shell would be to the non-initiator, the sooner the exchange took place, i.e. the sooner the non-initiator came up out of its shell. It appears that both shell weight and volume are important factors in determining non-initiator behaviour, as was shown earlier for initiators (Hazlett 1970). None of the variables representing initiator motivational levels were significant in explaining the variance in interaction length. That is, neither the deviations of the initiator's shell from its preferred shell size nor the extent that deviation would be reduced by obtaining the other crab's shell were important in ex-

Table I. Variables Tested for Effect on Interaction Length

Variable †	Interactions involving exchange (n = 15)	No exchange occurred (n = 26)
Initiator's shell wt.—Initiator's preferred wt	NS	NS
Initiator's shell vol.—Initiator's preferred vol	NS	NS
Defender's shell wt.—Defender's preferred wt	*	**
Defender's shell vol.—Defender's preferred vol	NS	NS
Initiator's shell wt.—Defender's preferred wt	NS	NS
Initiator's shell wt.—Defender's preferred vol	*	**
Defender's shell wt.—Initiator's preferred wt	NS	NS
Defender's shell vol.—Initiator's preferred vol	NS	NS

Significant effects at 0.05 = \*, significant effect at 0.01 = \*\* from analysis of variance.

† Absolute value of difference.

plaining interaction length (although as shown earlier (Hazlett 1970) initiators in all interactions gain in shell fit if an exchange occurs).

The most important point resulting from this analysis is that motivational variables associated with the non-initiator were more useful than those associated with the initiator in explaining variance in interaction length. The motivation of the non-initiator was correlated with interaction length, while variation in the motivational level of the initiator was not correlated with interaction length. This strongly indicates that the length of the interaction is determined by the behaviour of the non-initiator. When the non-initiator had less to lose or something to gain from the exchange, the interaction was indeed short when an exchange took place. The improvement in the shell fit of the non-initiator that would have occurred if an exchange took place was different in the two classes of interactions. When an exchange occurred, the non-initiator reduced the deviation from its preferred shell size by an average of 2.1 g and 1.7 ml of internal volume. When no exchange occurred the potential improvements averaged 0.3 g and 0.4 ml ( $t = 3.4$  and  $3.7$ , both  $P < 0.01$ , comparing non-initiator improvement in interactions involving exchange with those not involving exchange). The fact that the overall improvements in shell fit did not correlate with interaction length while specific motivational factors (present weight deviation and future volume deviation) of the non-initiator did correlate indicates that further work is needed to understand this system.

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#### Rodents' Defence Against Cigarette Smoke

Various laboratory rodents were exposed to tobacco smoke in an inhalation toxicity study. Unexpectedly, many animals responded by placing faeces in the smoke-delivery tubing, repeatedly and in quantity. One hamster stuffed the inlet so effectively that it suffocated and the method of exposure was changed.

'Air-inlet blocking' was first seen on day 2 of a 3-week study (experiment 1), and on day 4 a rat responded within 10 s of entering the cylinder. Blocking was seen at least once in six of the eight rats, 10 of 12 hamsters, and 10 of 16 mice, but in none of the eight guinea-pigs.

The animals were of both sexes and all but the hamsters were albinos. They were exposed singly in glass cylinders graded in size so that the occupant could just turn round. Standard puffs of cigarette smoke were diluted 1 : 100 in clean air. This was delivered through PVC tubing for 4 h each weekday and escaped through a capillary in the rubber bung closing each cylinder.

I have observed something of the development of this behaviour (experiment 2). First hamsters and then rats had five sessions in three of the largest cylinders (75 mm diameter, about 750 ml), through which air flowed at about 0.7 litre min<sup>-1</sup>; at the inlet, this is a speed of only about 0.6 km h<sup>-1</sup>. Starting midway through the second sessions, a cigarette was smoked at approximately hourly intervals, burning continuously for 3 to 4 min; the air carrying the smoke was diluted 1 : 10.

Before exposure to smoke, inlet-blocking did not occur. Animals entered the cylinders readily, defaecated and urinated rarely, and spent most time resting or asleep. Single actions were seen that were later used in blocking: digging on the glass floor (scraping and kicking backwards with fore- and hindlegs, push-digging forwards with the forepaws), biting at the corner of the air-inlet or the rubber bung. Faecal pellets or rubber chips were kicked haphazardly back and forth or carried in the mouth, especially before or after sniffing the air-inlet.